GROWTH AND DEVELOPMENT OF THE WESTERN HARVEST MOUSE, REITHRODONTOMYS MEGALOTIS MEGALOTIS

Gary H. Richins^{1,2}, H. Duane Smith¹, and Clive D. Jorgensen¹

ABSTRACT.— Growth rates, gestation period, litter size, reproductive age, sex ratios, and development were studied on 198 litters of *Reithrodontomys megalotis megalotis* (Baird). Growth was characterized by several standard skull and body measurements and was partitioned into four phases of 1-3, 4-12, 13-22, and 23-70 days. Growth was best described by measurements of tail length, ear length, and dried eye-lens weight.

Reproductive activity began as early as 38 days for females and 59 days for males. The gestation period was 22 days, and the mean litter size was 3.83 (range 1-7). Sex ratio was 53.49 percent males to 46.51 percent females. Reproductive efficiency was 53.53 percent. The development of R. m. megalotis was very similar to that of R. m. dychei.

Early breeding, postpartum estrous, year-round breeding, high reproductive efficiency, and a short gestation period contribute to a high reproductive potential in R. m. megalotis.

Small mammals occupy vital positions in the bioenergetics of North American deserts because they are important primary consumers, but many of their interactions within the ecosystem are not understood. Productivity estimates of rodent populations seldom take into account the biomass and biotic potential of young animals, especially when these estimates are made solely on the basis of trappable animals with disregard for such dynamic variables as litter size, gestation period, reproductive age, sex ratios, and biomass.

Because this type of data is difficult to obtain in the field, it is usually provided by laboratory studies. This study will define the growth and development of *Reithrodontomys megalotis megalotis* (Baird), a small cricetine found throughout much of North America.

The objectives of this study are (1) to characterize growth from birth to maturity by measurements of various body and skull parameters, (2) to determine gestation period, litter size, reproductive age, sex ratios, and development of behavioral sequences, and (3) to correlate these data, where possible, with similar studies on related species.

LITERATURE REVIEW

Growth rates have been studied for several small mammals (e.g., Meyer and Meyer, 1944; Pournelle, 1952; Chew and Butterworth, 1959; Layne, 1960; Goertz, 1965; Hayden and Gambino, 1966; Jones, 1967; Horner and Taylor, 1968), but *Reithrodontomys*, particularly *R. megalotis*, remains basically unstudied. Life histories of *R. humulis* (Holding and Royal, 1952; Layne, 1959; Kaye, 1961), *R. montanus* (Leraas, 1939), *R. fulvescens* (Svihla, 1950), and

¹Department of Zoology, Brigham Young University, Provo, Utah 84602 ²Currently Wildlife Biologist, Dames and Moore, Cincinnati, Ohio

R. megalotis (Svihla, 1931; Smith, 1939; Brummel, 1961) have been partially studied. Bancroft (1966) completed an intensive study of reproduction, development, and behavior of *R. megalotis dychei* from Kansas, but no correlation of age with growth was attempted, nor has Bancroft's (1966) information been published.

MATERIALS AND METHODS

Animals used in this study were reared from 20 pairs of R.m.megalotis captured approximately 19 km SE of Benmore Guard Station, Tooele Co., Utah, from 1-9 September 1971 and subsequently housed in a laboratory at Brigham Young University. The animals were caged in standard small-mammal cages with wood shavings provided as substrate and cotton as nesting material. Free water and Purina mouse breeder chow were available continuously. Laboratory temperature was held at 22 ± 2 C with a photoperiod of 12 hr. light and 12 hr. dark; varying intensities simulated dawn and dusk. Animals brought into the laboratory were sexed, paired, and checked daily for food, water, and presence of a litter.

When a litter was born, each litter member was marked by sequential toe clipping. The following measurements were taken daily from days 1-22 and then weekly for 7 additional weeks on a sample of 100 animals: (1) body weight, (2) total length, (3) tail length, (4) ear length from notch, and (5) hind-foot length. Daily observations on development and behavior were recorded for each litter. Body weight was determined to the nearest 0.05 g; total and tail lengths, to the nearest 0.5 mm; and ear and hind-foot lengths, to the nearest 0.01 mm. After the eyes had opened and the individuals had become more active (about 10 days of age), they were anesthetized with Penthrane.³

Ten individuals were killed daily from 1 to 22 days and weekly from 4 to 10 weeks for additional studies on skull measurements and eye lens weights to correlate age with the external measurements. On the day that an animal was to be killed, it was removed from the nest and administered a lethal dose of Penthrane. Standard body measurements were taken and the carcass placed in a 10percent formalin solution to fix the eye lenses. After four days the carcass was taken from the formalin solution; the head was removed and skinned; and the lenses were extracted with a curved forceps after a slit had been made in the cornea. The lenses were stored in vials of 10-percent formalin, after which they were dried at 100 C for one week before weighing to the nearest .0001 g.

After the lenses had been extracted, the skull was stained and the (1) total length, (2) zygomatic breadth, (3) foramen magnum height, (4) mastoidal breadth, (5) nasal length, and (6) cranium width were measured to the nearest 0.01 mm with dial calipers. Staining followed the methods described by Humason (1967), except that the concentration of alizarine stock solution used was increased 10 times.

³Abbott Laboratories, North Chicago, Illinois.

The instantaneous relative growth rate (IGR) described by Brody (1945) and Lackey (1967) was calculated to express growth as a rate between times of measurement and percentage of adult size. The IGR is expressed as dW/dt/W, where W is the parameter measured at the instant the rate of change of dW/dt is measured. Because it is not entirely possible to develop the "instantaneous" rate of growth, it was necessary to integrate the infinite number of growth rates to derive $W = Ae^{kt}$. This is conveniently written as $\ln W = \ln A + kt$ where: $\ln W$ is the natural logarithm of the variable measured (W) at t = 0, $\ln A$ is the natural logarithm of a theoretical constant based on the value of W at t = 0, k represents the instantaneous relative growth rate (when multiplied by 100, k = percentage growth rate), and t is time (age in days). For comparative purposes, the IGR (k) is determined with

$$k_n = \frac{\ln W_n - \ln W_{n-1}}{t_n - t_{n-1}}$$

Thus k is definite and can be used to compare differences in rates of growth.

Reproductive efficiency, defined as the weight of the litter multiplied by 100 and divided by the weight of the mother (Kaye, 1961) was determined for 19 adult female R. m. megalotis. In all instances both measurements were taken immediately after birth.

RESULTS AND DISCUSSION

Growth Rates

The instantaneous relative growth rates k for body weight, total length, tail length, ear length, and hind-foot length that were determined each day for 100 R. m. megalotis from 1 to 22 days and then weekly for the next 7 weeks are reported in Table 1. Growth rates (k) were also calculated for dried eye-lens weight, skull total length, zygomatic breadth, foramen magnum height, mastoidal breadth, nasal length, and cranium width on 10 animals each day from 1 to 22 days and then weekly for the next 7 weeks. This reduction in sample size from 100 to 10 per day was necessary, owing to the time required to raise animals to the proper age and to prepare the skulls and lenses.

Previous studies (Smith and Jorgensen, 1972) involving computer analyses of growth data using linear, quadratic, cubic, combined linear-quadratic, and combined linear-quadratic-cubic distributions with different time intervals were conducted to characterize species growth curves. Since the growth curves turned out to be curvilinear, none of the time intervals used with the above distributions and combinations of distributions adequately described the entire growth curve for any parameter. Brody's (1945) logarithmic approach adopted in this paper and used by Smith and Jorgensen (1973), however, does accurately describe the growth of R. m.

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k	10 n = 100	001271 880845 170411 1410157		9 .1055 11 .0945 57 .0414 5 .0038			2010
	n = 10	.1300 .0848 .0487 .0487	.086 .002 .002 .002	.132 .105 .046		.0929 .0577 .0194	.4867 .1820 .0337 .0159
lnA	n = 100	0.2482 0.4029 0.8676 1.8053	3.7609 3.7895 4.0837 4.7579	2.3960 2.4496 3.0958 4.0245	$\begin{array}{c} 0.3730 \\ 1.0368 \\ 1.4669 \\ 2.5732 \end{array}$	$\begin{array}{c} 1.8136 \\ 1.9031 \\ 2.4023 \\ 2.8252 \end{array}$	
	n = 10	0.4087 0.6668 0.9555 1.9007	3.7444 3.8684 4.1701 4.8253	2.3621 2.5983 3.2106 4.1493	$\begin{array}{c} 0.3022\\ 1.1064\\ 1.5477\\ 2.6303\end{array}$	$\begin{array}{c} 1.8138 \\ 2.0453 \\ 2.4590 \\ 2.8773 \end{array}$	-9.6263 -8.6041 -6.9336 -6.7643
Age in Davs	(t=t-1)	1-3 4-12 13-22 23-70	1-3 4-12 13-22 23-70	1-3 4-12 13-22 23-70	1-3 4-12 13-22 23-70	1-3 4-12 13-22 23-70	1-3 4-12 13-22 23-70
	Parameter	Body Weight	Total Length	Tail Length	Ear Length	Hind-Foot Length	Dried Eye-Lens Weight

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Skull Total Length	1-3 4-12 13-22 23-70	2.2411 2.3662 2.6658 2.8731	.0683 .0371 .0113 .0017	.2656 .6839 .1985 .2810
Zy gomatic Breadth	1-3 4-12 13-22 23-70	1.6980 1.8599 2.0332 2.2512	.0496 .0266 .0106 .0006	.1116 .5816 .1004 .0293
Foramen Magnum Height	1-3 4-12 13-22 23-70	0.7337 0.8292 1.0644 1.2950	.0570 .0297 .0008 .0008	.0517 .4024 .0835 .0136
Mastodial Breadth	1-3 4-12 13-22 23-70	1.5132 1.7198 2.0563 2.1200	.0326 .0346 .0033 .0002	.0457 .5563 .0454 .0040
Nasal Length	1-3 4-12 13-22 23-70	0.8588 1.0450 1.4497 1.8263	.0994 .0572 .0216 .0033	.4501 .7338 .6049 .1613
Cranium Width	1-3 4-12 13-22 23-70	1.7787 1.9281 2.1876 2.2845	.0461 .0268 .0044 .0001	.2434 .6096 .1397 .0014

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Table 1 (Continued)

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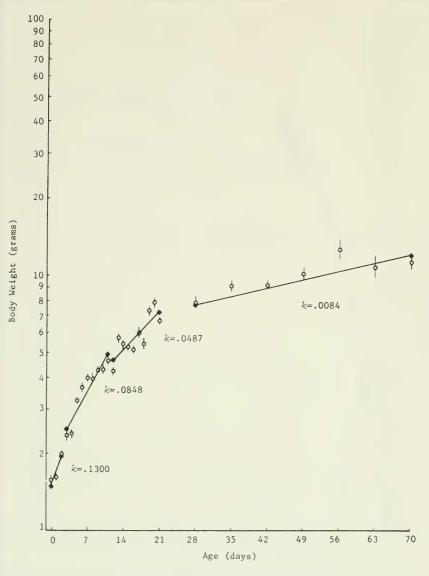
megalotis for the time intervals (growth phases) 1-3, 4-12, 13-22, and 23-70 days.

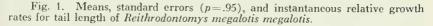
Not only is growth characterized by these four time intervals, but developmental sequences also tend to correspond to them. From 1 to 3 days the young harvest mouse is adjusting to the rigors of life outside the uterus. Because there is a rapid elongation of the extremities and a constant gain in weight (Figures 1-4), but little visible external development, there is probably considerable internal change taking place. During the 4-12-day growth phase, however, a great deal of external change is manifest. The extremities and body continue to elongate, and the animal increases in weightalthough at a slower rate (Figures 1-4). The ears unfold, and the pinnae begin to develop. The toes separate and become functional. Pelage develops, and the teeth erupt from the gums. The eyes open, and there is increased activity about the nest. The external auditory meatus opens, and the sense of hearing develops. Little external change other than a continued elongation of the extremities (Figures 1-4) characterizes the 13-22-day growth phase. Near the beginning of this period the young animals begin to take solid food, and by 22 days of age they are completely weaned. From 23 to 70 days the growth of extremities all but ceases, and body weight is stabilized (Figures 1-4). Sexual development proceeds, and by 70 days both sexes have reached maturity.

The \mathbb{R}^2 values (Table 1) indicate the amount of variation accounted for by growth of the parameter during a particular time interval. When \mathbb{R}^2 values are converted to r, they indicate statistical significance. When time is partitioned into growth phases, a significant r indicates correlation between $\ln W$ and age and is used to establish confidence in k.

Tail length, ear length, and dried eye-lens weight provided the best correlations of relative growth with age (Table 1), r being significant during all four growth phases (n=10). Although dried eye-lens weight was the best indicator of growth—and, ultimately, of age—in the laboratory, tail length or ear length would be the best parameter to measure in the field because these measurements are easily taken and do not involve killing the animal. Significance was spotty among the other parameters for the various growth phases, but all of the parameters were significantly correlated with age during the 4-12 day interval when the majority of growth and development occurred.

Graphic representations of means, standard errors, and instantaneous relative rates (k) were prepared for the three most significant growth parameters—tail length (Fig. 1), ear length (Fig. 2), and dried eye-lens weight (Fig. 3) as well as for body weight (Fig. 4). The close correlation of k with the actual data means indicates that the k values for each of the four growth phases characterize the growth of R. m. megalotis. If a detailed growth analysis as is presented here is unfeasible, a workable growth curve could be presented using the means and standard errors; but it is imperative that these be plotted on a logarithmic scale for the curve to be meaningful.





The presence of four growth phases (1-3, 4-12, 13-22, and 23-70 days) in *R. m. megalotis* differs from the results of other workers. Layne (1959) found two growth phases in *R. humulis*: 0-3 weeks and 3-7 weeks. Bancroft (1966) found three growth phases in *R. m. dychei*: 0-3 weeks, 3-7 weeks, and 7-10 weeks.

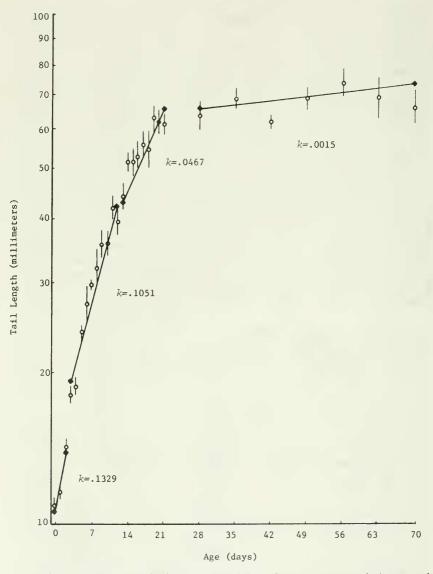
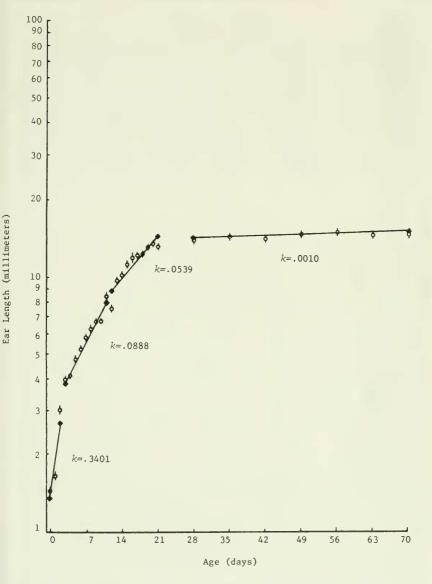
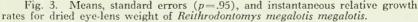


Fig. 2. Means, standard errors (p=.95), and instantaneous relative growth rates for ear length of *Reithrodontomys megalotis megalotis*.

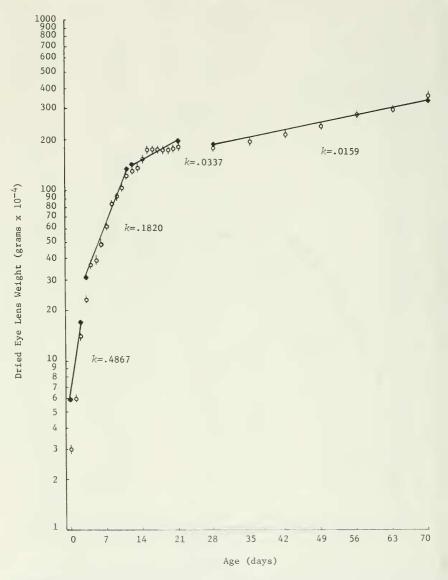
Age prediction

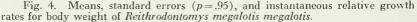
Because the correlation of some growth parameters with age is significant, one might consider using these parameters to predict age. Although the process seems evident at first (it would involve simply reading the predicted age from a graph), the results cannot





be interpreted with statistical confidence because of the lack of variation among days. Calculation of confidence limits about the regression line presents special problems, because the X axis (age) is a non-random variable, selected arbitrarily by the investigator; thus, only the regression of Y on X can be estimated with confidence.





When a least squares regression equation is used to predict ages of unknown animals, age becomes a random variable (Dapson and Irland, 1972; Smith and Jorgensen, 1972); consequently, the analyses of these data to provide age determinations await nonparametric procedures.

Gestation Period

The minimum gestation period of 22 days, as determined by the minimum interval between successive litters, was shorter than previously reported: Svihla (1931) reported 23 days and EcoDynamics (1971) reported 25-28 days as the gestation period for R. m. megalotis. One litter was born after only 20 days, but because all four young died within a few hours, the litter was assumed to be premature. Our results are similar to those of other workers. Bancroft (1967) reported 23 days as the gestation period for R. m. dychei, while Layne (1950) listed 24 days for R. humulis, although later Kaye (1961) reported 21 days. Leraas (1938) reported 21 days as the gestation period for R. montanus.

Litter Size

Litter size had a mean of 3.83 and ranged from 1 to 7 (Table 2), which is comparable to Bancroft's (1966) reporting of 3.84 and a range of 1-7 for R. m. dychei, although litter size had been stated earlier by Long (1962) to include up to nine. Svihla (1931) listed an average litter size of 2.60, ranging from 1 to 7, for R. m. ni-grescens and R. m. megalotis. Other findings on litter size of R. megalotis vary somewhat, although always within the ranges previously stated: 4-6 in Oregon (Bailey, 1936); 1-4 and a mean of 2.0 in South Dakota (Zukerman, 1935); 1-7 for captive bred, with a mean of 4.27, and up to eight for laboratory bred (Egoscue, Bittmenn and Petrovich, 1970; Egoscue, 1972). Egoscue (1972) further reported an average litter size of 5.64 for wild caught females, ranging from 3 to 6, based on embryo counts of 56 placenta examinations.

Litter size varied with the number of litters females had already produced. The mean litter size (3.29) of 69 first litters of R. m.megalotis increased to 4.71 for 17 fourth litters before decreasing to 3.60 for five ninth litters (Table 2). Bancroft (1966) stated that mean litter size of three R. m. dychei was 4.30 for first litters, increased to a maximum of 6.00 for fifth litters, and decreased to a low of 3.30 for eleventh litters. This would indicate that female R. m.megalotis reach their maximum reproductive capabilities from 20-25 weeks of age—assuming that most are bred by 10 weeks and produce a new litter approximately every 3-3.5 weeks. While this reproductive rate is possible under laboratory conditions, it is likely to proceed more slowly in a field situation in which successful male-female encounters are logistically reduced.

Sex Ratio

The sex ratios of newly born R. m. megalotis resulted in 53.5 percent males and 46.5 percent females (Table 2). This sex ratio varies from those previously reported. Egoscue (1972) lists a sex ratio of 50.99 percent males to 49.01 percent females for 901 R. m. megalotis, whereas Bancroft (1966) reports a sex ratio at birth of 51 percent males to 49 percent females for 438 R. m. dychei. Layne

Successive	Number	Average			Percentage	
Litter Number	of Litters	Litter Size	Males	Females	Males	Females
1	69	3.29	1.90	1.39	52.7	42.3
2	37	3.86	2.24	1.62	58.0	42.0
3	30	4.23	1.90	2.33	44.9	55.1
4	17	4.71	2.76	1.94	58.8	41.2
5	12	4.25	2.17	2.08	50.9	49.1
6	10	4.10	1.80	2.30	43.9	56.1
7	9	4.00	2.00	2.00	50.0	50.0
8	8	3.88	2.00	1.88	51.6	48.4
9	5	3.60	1.60	2.00	44.4	55.6
10	1	5.00	2.00	3.00	40.0	60.0
1-10	198	3.83	2.05	1.78	53.49	46.51

TABLE 2. Mean Number of Young *Reithrodontomys megalotis megalotis* Born in the Laboratory per Successive Litter.

(1959) found an even sex ratio at birth in R. humulis, but Kaye (1961) reported a ratio of 33.4 percent males to 66.6 percent females for 27 R. humulis.

Reproductive Age

Svihla (1931) reported 128 days as the youngest age at which a male or female R. m. megalotis had been found to breed. Leraas (1938) found that female R. montanus albescens gave birth as early as 90 days. Layne (1959) reported that one female R. humulis humulis became pregnant at 77 days and that males had enlarged testes as early as 49-50 days. Bancroft (1966) listed one female R. megalotis dychei as giving birth at 72 days and males as reaching sexual maturity at from 56 to 70 days.

During this study of R. m. megalotis, a female 29 days old was paired with a male 50 days old. This pairing resulted in a litter of four young born when the female and male parents were 62 and 83 days of age respectively. Granting a 22-day gestation period, R. m.megalotis can become reproductively active as early as 38 days and 59 days for females and males respectively, which supports the 35 days reported but unpublished by EcoDynamics (1971) but which supplants previously published data.

Reproductive Efficiency

R. megalotis has the highest reproductive efficiency reported for any mammal (Bancroft, 1966). Reproductive efficiency was calculated for 19 adult female *R. m. megalotis* resulting in a high of 53.33 percent for a litter of six. The mean reproductive efficiency of the 19 animals was 43.44 ± 2.91 percent (31.5-53.3 percent). Frank (1956) listed *Microtus arvalis* as having the highest reproductive efficiency of any mammal, the litter weight amounting to 53.2 percent of the mother's weight, but Bancroft (1966) reported 62.5 percent for a litter of five *R. m. dychei*. Kaye (1961) listed a high 50.5 percent for *R. humulis*. Dunaway (1962) listed 77.7 percent as the reproductive efficiency of a litter of eight R. humulis, but because the measurements were taken some 10-15 hours after birth, it is probably erroneous.

Reproductive Potential

Several of the foregoing factors contribute to the high reproductive potential of *R. megalotis*: early breeding, postpartum estrous, year-round breeding, high reproductive efficiency, and a short gestation period.

Early breeding allows for a longer reproductive life. Postpartum estrous which was evidenced during this study enables R. m. megalotis to maximize the number of litters born during a single season. In Utah the breeding season runs from mid-May to early September. Therefore, a harvest mouse born in early June could have as many as two litters its first year. A mature harvest mouse could have 4-5 litters during this time and could contribute 15-20 individuals to the population in a single year.

A high reproductive efficiency allows a greater percentage of energy intake to go for reproduction, thus maximizing reproductive potential. A short gestation period in concert with postpartum estrous is also advantageous because it tends to minimize the time between successive litters.

Reproductive potential for any species is clearly a function of litter rapidity and the length of time reproductive activity occupies in the life span of females. Under laboratory conditions, these factors can be maximized, although field conditions obviously impose yet another constraint—environmental limits, including population interactions. Bancroft (1966) reported postpartum estrous in R. m. dychei; and, although they can breed year-round in the laboratory, he doubts this would persist in nature, except perhaps in the southern part of their range.

Development

Condition at birth. Neonatal R. m. megalotis are similar in appearance to R. m. dychei (Bancroft, 1966) in that they are smooth and pink and are naked except for natal vibrissae. Eyes are closed and covered with a transparent membrane, including the crease marking the persisting fusion of upper and lower eyelids. Pupils are clear, with the exception of coloration in the iris. Ear pinnae are folded and appressed against the head. Toes are still fused, and nails are not yet present. The young vocalized faintly when handled.

One day. There is little morphological change, although the ear pinnae are sometimes unfolded. A gray dorsal stripe is visible, and the skin has lost its newborn transparency. Hair is not evident, although Bancroft (1966) reported fine hair visible upon close examination of the dorsum in R. m. dychei. Layne (1959) also noted abundant short and long hair on the dorsum of day-old R. humulis.

Two days. Ear pinnae have unfolded, and the dorsal pigmentation is darker, with dorsal hairs visible when held to the light. Toes are about one-third separated and claws are visible. Young move their feet rapidly and vocalize sharply when handled.

Three days. The young cling to the female's nipples and are often dragged around the cage several times before falling off when disturbed. Vocalization is a high-pitched squeak, 2-8/second. The toes are about one-half separated. Eyelid slits are visible. The dorsal pigmentation is almost black, and a white, scaly epidermal material observed by Bancroft (1966) in R. m. dychei and by Layne (1959) in *R. humulis* is present on the dorsum. Four days. The toes are almost separated. The hair on the head

is thicker and colored a pale gray brown. Bancroft (1966) stated that at this age R. m. dychei had claws approximately 5 mm long and that the ears were only fleshy lobes.

Five days. Dorsal furring extends about one-third of the way along the back, and the upper and lower incisors have erupted in some. Bancroft (1966) stated that the lower incisors had erupted in R. m. dychei. Layne (1959) also reported that the lower incisors were visible in R. m. megalotis on the fifth day.

Six days. There is little external change evident, although Ban-croft (1966) reported that hair had appeared on the dorsal side of the tail in *R. m. dychei*.

Seven days. The dorsum is completely furred, and ventral hair is more pronounced. Mammae are visible in females.

Eight days. The external auditory meatus is open, and the young are very active and vocal. Opening of the external auditory meatus almost always precedes the opening of the eyes by one day.

Nine days. The venter, feet, and pinnae are completely furred, and the eyes are beginning to open. Smith (1936) reported that the eyes first opened at six days but were of little use for 48 hours. Bancroft (1966) found that the eyes were beginning to open in R. m. dychei at seven days but were not yet fully functional. Svihla (1931) found that the eyes opened on days 11-12 in R. m. megalotis, as did Brummel (1961). Leraas (1938) observed that the eyes opened on the eighth day in R. montanus. Layne (1959) reported that the eyes opened at from 7 to 10 days in R. humulis. In the present study, the eyes of R. megalotis megalotis opened at from 9 to 13 days.

Ten days. The eyes are open and fully functional in the ma-

jority of the young. Fourteen days. Face washing is observed. There is very little started eating solid food.

Sixteen days. Although nursing is observed until the sixteenth day, the majority of the young are completely weaned. There is no detectable change in appearance or behavior on days 11, 12, 13, and 15.

SUMMARY AND CONCLUSIONS

The growth date of R. m. megalotis can be divided into four distinct phases: 1-3, 4-12, 13-22, and 23-70 days; whereas R. m. dychei and R. humulis humulis have three and two growth phases respectively (Bancroft, 1966; Layne, 1959). Growth of R. m. megalotis through all four phases is most accurately characterized by tail length, ear length, and dried eye-lens weight measurements.

R. m. megalotis had a 22-day gestation period, one day shorter than previously reported. Litter size varied from 1 to 7, and sex ratios at birth were approximately even.

Western harvest mice became reproductively active earlier than previously reported. One R. m. megalotis became pregnant at 38 days of age.

A high reproductive efficiency, 53.33 percent in this study and 62.5 percent (Bancroft, 1966), has been evidenced in R. m. megalotis.

R. m. megalotis has a high reproductive potential because of early breeding, postpartum estrous, year-round breeding, high reproductive efficiency, and a short gestation period.

The development of R. m. megalotis closely followed that of R. m. dychei as reported by Bancroft (1966), but differed slightly in that the eyes opened at from 9 to 13 days in R. m. megalotis while in *R. m. dychei* the eyes opened at from 7 to 11 days.

In the laboratory R. m. megalotis grows faster, has a shorter gestation period, has larger litters, breeds earlier, and has a higher reproductive efficiency than previously reported for this genus.

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